SHORTER ARTICLES AND DISCUSSION

A BIOLOGICAL SURVEY OF DESCRIBED CERCARIÆ IN THE UNITED STATES*

AMONG the earlier American zoologists Joseph Leidy alone was a student of cercariæ. From his time to very recent years American cercariæ have received little attention. This may have been due to the greater demands made by other groups of animals, or possibly to the minute size of the larvæ and a failure to appreciate the exact differences of their structure. It could not have been due to a lack of knowledge of the presence of cercariæ, for the European records were abundant and the classical studies of Leuckart, Ercolani and Looss had demonstrated the life-history relations of cercariæ and adult flukes. Moreover, the large number of adult trematode records showed that the larvæ must be fairly abundant.

Within the past few years a revival of study in this larval group has revealed a large number of forms, so that now there are some sixty named species. Only eight of these have dates prior to 1914. The majority of described cercariæ have been worked over by Cort, Faust and O'Roke.

A study of the descriptions of earlier named species shows them to be very general, so that they apply not to the species at all but to larger groups, genera or perhaps even subfamilies. For example, the record of a monostome with three eye-spots instead of characterizing a species merely distinguishes the trioculate from the binoculate group of species. A parallel is found in the diplostomulum commonly known as *Diplostomum cuticula* von Nordmann 1832, which has been recorded from a variety of vertebrate hosts and from equally variable habitats. There is great probability of the existence of several new species concealed beneath these generalized data. Such cases illustrate the futility of generalized descriptions.

Cort emphasizes the value of the excretory system of the cercaria as a basis of description. The conservatism of the system is urged as a basis on which fundamental group relationships of the trematodes can be discovered. Advantage in using this

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TABLE I

Record of Described Cercariæ in the United States

Name	Host	Locality and Date	Per Cent. Infection
Monostomes			
1. *C. urbanensis* Cort, 1914	*Physa gyrina* Say	Urbana, Ill., 1913	5.0
2. *C. konadensis* Faust, 1917	*Lymnæa proxima* Lea	Corvallis, Mont., 1916	31.3
3. *C. pellucida* Faust, 1917	*Physa gyrina* Say	Ft. Missoula, Mont., 1916	5.5
4. *C. pellucida* Faust, 1917	*Lymnæa proxima* Lea	Corvallis, Mont., 1916	31.3
5. *C. robusta* Faust, 1918	*Physa gyrina* Say	DeKalb, Ill., 1917	60.0
6. *C. aurita* Faust, 1918	*Goniobasis pulchella* (Anthony)	Homer, Ill., 1917	8.3
7. *C. hyalocauda* Haldeman, 1842	*Physa heterostropha* (Say)	Philadelphia, Pa., 1842 ?	?
8. *C. hyalocauda* Haldeman, 1842	" " "	Philadelphia, Pa., 1880	?
9. *C. lucania* Leidy, 1877	*Planorbis parvus* Say	Philadelphia, Pa., 1877 ?	Heavy
Amphistomes			
10. *C. inhabilis* Cort, 1914	*Planorbis trivolvis* Say	Lawrence, Kan., 1913	11.1
11. *C. inhabilis* Cort, 1914	" " "	Urbana, Ill., 1913	Few
12. *C. inhabilis* Cort, 1914	" " "	Lawrence, Kan., 1915	4.5
13. *C. diastropha* Cort, 1914	" " "	Chicago, Ill., 1913	5.0
14. *C. diastropha* Cort, 1914	" " "	Lawrence, Kan., 1915	4.0
15. *C. cortii* O'Roke, 1917	" " "	Cherryvale, Kan., 1915	4.0
16. *C. gorgonocephala* Ward, 1916	Free in plankton, host unknown	Put-in-Bay, O., 1901	Single specimen
Distomes			
17. *C. megalura* Cort, 1914	*Pleurocerca elevatum* Say	Sangamon River, Ill., 1913	1.4
18. *C. megalura* Cort, 1914	*Goniobasis virginica* Say	Princeton, N. J., 1908	?
19. *C. gracilescens* Faust pro *C. gracilis* O'Roke, 1917, preocc.	*Physa integra* Hald.	Chanute, Kan., 1915	4.0
20. *C. magnacauda* O'Roke, 1917	*Planorbis trivolvis* Say	Lawrence, Kan., 1915	5.0
21. *C. agilis* Leidy, 1858	"In company with *Planorbis*, *Paludina*, and *Lymnæa*"	Delaware, R., ?	?
22. *C. ascoidea* Leidy, 1877	*Planorbis parvus* Say	Philadelphia, Pa., 1877 ?	Heavy
23. *C. ascoidea* Leidy, 1877	*Lymnæa elodes* Say	Philadelphia, Pa., 1877 ?	?
24. *C. trigonura* Cort, 1914	*Campeloma decisum* (Say)	Hartford, Conn., 1913	11.0
25. *C. wrightii* Ward, 1916	In aquarium, host unknown	Toronto, Can., 1885	Single specimen

TABLE I—*Continued*

Name	Host	Locality and Date	Per Cent. Infection
Distomes			
26. *C. anchoroides* Ward, 1916[1]	Free-swimming, host unknown	Lake St. Clair, 1894	—
27. *C. douthitti* Cort, 1914	*Lymnæa reflexa* Say	Chicago, Ill., 1913	10.3
28. *C. douthitti* Cort, 1914	*Lymnæa stagnalis appressa* Say	Douglas Lake, Mich., 1915–1916	?
29. *C. douthitti* Cort, 1914	*Lymnaa stagnalis perambla* Walker	Douglas Lake, Mich., 1915–1916	?
30. *C. gracillima* Faust, 1917	*Physa gyrina* Say	Bitter Root River, Mont., 1916	19.4
31. *C. gracillima* Faust, 1917	*Lymnæa proxima* Lea	Missoula, Mont., 1916	3.1
32. *C. tuberistoma* Faust, 1917	*Physa gyrina* Say	Corvallis, Mont., 1916	5.3
33. *C. gigas* Faust, 1918	*Planorbis trivolvis* Say	DeKalb, Ill., 1917	56.0
34. *C. gigas* Faust, 1918	" "	Urbana, Ill., 1917	100.0
35. *C. gigas* Faust, 1918	*Physa gyrina* Say	Pine Creek, Ill., 1917	23.0
36. *C. minima* pro *C. minor* Faust, 1918 preocc.	" " "	DeKalb, Ill., 1917	6.0
37. *C. inversa* O'Roke, 1917	" " "	Lawrence, Kan., 1915	2.0
38. *C. echinocauda* O'Roke, 1917	" " "	Lakeview, Kan., 1915	6.0
39. *C. quieta* O'Roke, 1917	*Planorbis trivolvis* Say	Lawrence, Kan., 1915	15.4
40. *C. elephantis* Cort, 1918	" "	Douglas Lake, Mich., 1914–1916	?
41. *C. emarginatæ* Cort, 1918	*Lymnæa emarginata angulata* Sowerby	Douglas Lake, Mich., 1914–1916	?
42. *C. douglasi* Cort, 1918	*Physa ancillaria* Say	Douglas Lake, Mich., 1914–1916	?
43. *C. tardigrada* Leidy, 1858	*Anodonta (fluviatilis) cataracta* Say	Philadelphia, Pa. ? ?	?
44. *C. tardigrada* Leidy, 1858	*Anodonta (lacustris) marginata* Say	Philadelphia, Pa. ? ?	?
45. *Cercariæum helicis* Leidy, 1847	*Helix albolabris* Say	Philadelphia, Pa. ? ?	?
46. *C. helicis* Leidy, 1847[2]	*Helix alternata* Say	Philadelphia, Pa. ? ?	?
47. *C. leptacantha* Cort, 1914	*Campeloma decisum* Say	Hartford, Conn., 1913	8.3
48. *C. caryi* Cort, 1914	*Goniobasis virginica* Say	Princeton, N. J., 1909	?
49. *C. brevicæca* Cort, 1914	*Physa anatina* Lea	Manhattan, Kan., 1913	3.2
50. *C. crenata* Faust, 1917	*Lymnæa proxima* Lea	Ft. Missoula, Mont., 1916	13.6
51. *C. isocotylea* Cort, 1914	*Planorbis trivolvis* Say	Urbana, Ill., 1914	18.0
52. *C. isocotylea* Cort, 1914	" "	Urbana, Ill., 1916–1917	50.0
53. *C. isocotylea* Cort, 1914	" "	DeKalb, Ill., 1917	6.0
54. *C. polyadena* Cort, 1914	*Lymnæa reflexa* Say	Chicago, Ill., 1913	2.6

TABLE I—*Continued*

Name	Host	Locality and Date	Per Cent. Infection
Distomes			
55. *C. dendritica* Faust, 1917	*Lymnæa proxima* Lea	Ft. Missoula, Mont., 1916	35.7
56. *C. dendritica* Faust, 1917	" " "	Bitter Root River, Mont., 1916	10.3
57. *C. glandulosa* Faust, 1917	*Physa gyrina* Say	Corvallis, Mont., 1916	40.0
58. *C. diaphana* Faust, 1917	*Lymnæa proxima* Lea	Corvallis, Mont., 1916	31.3
59. *C. micropharynx* Faust, 1917	" " "	Missoula, Mont., 1916	56.3
60. *C. racemosa* Faust, 1917	" " "	Ft. Missoula, Mont., 1916	10.3
61. *C. hemilophura* Cort, 1914	*Physa gyrina* Say	Rockford, Ill., 1913	5.0
62. *C. stilifera* Faust, 1918	" " "	Pine Creek, Ill., 1917	6.6
63. *C. haskelli* O'Roke, 1917	" " "	Lawrence, Kan., 1915	3.0
64. *C. gregaria* O'Roke, 1917	*Planorbis trivolvis* Say	Cherryvale, Kan., 1915	21.7
65. *C. kansiensis* O'Roke, 1917	" " "	Pratt, Kan., 1915	75.0
66. *C. Lissorchis fairporti* Magath, 1918	" " "	Fairport, Iowa, 1917	10.0
67. *C. platyura* Leidy, 1890	*Lymnæa* sp.?	Fort Bridger, Wyo. ?	Free in pool
68. *C. reflexæ* Cort, 1914	*Lymnæa reflexa* Say	Chicago, Ill., 1913	21.0
69. *C. rubra* Cort, 1914[3]	*Campeloma decisum* (Say)	Hartford, Conn., 1913	16.6
70. *C. trivolvis* Cort, 1914	*Planorbis trivolvis* Say	Urbana, Ill., 1913	Few
71. *C. trivolvis* Cort, 1914	" " "	DeKalb, Ill., 1917	23.3
72. *C. biflexa* Faust, 1917	*Physa gyrina* Say	Ft. Missoula, Mont., 1916	7.0
73. *C. trisolenata* Faust, 1917	" " "	Ft. Missoula, Mont., 1916	49.1
74. *C. trisolenata* Faust, 1917	*Planorbis trivolvis* Say	Ft. Missoula, Mont., 1916	75.0
75. *C. chisolenata* Faust, 1918	*Physa gyrina* Say	Pine Creek, Ill., 1917	8.3
76. *C. acanthostoma* Faust, 1918	" " "	Urbana, Ill., 1917	100.0
77. *C. acanthostoma* Faust, 1918	*Planorbis trivolvis* Say	Urbana, Ill., 1917	100.0
78. *C. fusiformis* O'Roke, 1917	*Physa gyrina* Say	Lawrence, Kan., 1915	1.0
Holostomes			
79. *C. flabelliformis* Faust, 1917	*Physa gyrina* Say	Corvallis, Mont., 1916	23.3
80. *C.* (*Tetracotyle*) *typica* Diesing, by Leidy, 1890	*Galba catascopium* (Say)	Philadelphia, Pa. ? ?	?
81. *C.* sp. by Rettger, 1896	*Lymnæa stagnalis* (Linn.)	Terre Haute, Ind. ?	?

[1] Recently the writer has described two species closely related to *C. anchoroides*: *C. brookoveri*, from Campeloma sp., Cedar Point, Lake Erie, 1912, and *C. macrostoma*, free in an aquarium, Urbana, Ill., 1917.

[2] Possibly Agamo distomum.

[3] Agamo distomum.

system lies in the fact that it can be studied entirely in the living cercariæ. The writer has used this method with profit, but in addition has worked out a method of staining the genital organs in the preserved larvæ. This method can be utilized when the worker has access only to preserved larvæ. While the excretory system is indeed a conservative system, the genital system is probably more conservative and less likely to change from cercarial to adult stage. It has been found to be remarkably similar in the large, yet variable in minor, details in groups of cercariæ known to be related through other organs or systems. The best description of a cercaria is probably that which includes both the excretory system as worked out in the living animal and the genital cell masses as depicted in carefully preserved and stained material.

A mere superficial description of the worm is a distinct burden on the literature. The cercaria should be carefully studied in minute detail or not at all. It is the nicety of technic and care in observation which have yielded the number of species now known and bids fair to increase the number vastly in the next few years. It is necessary, then, to urge the investigator in this group to use the utmost care in his work, to describe the minute parts of the organs, and to record the complete biological data available that these records may be of use in life-history investigations.

In order to place the more important biological data of described cercariæ in the United States in a convenient form, a table has been prepared to cover the groups, the authors and dates of the naming of the species, the hosts, localities and dates of collections and the per cent. of infection (see Table I). The same data have been collated from the standpoint of the host in Table II.

A study of the described species shows that the great bulk are distome larvæ. Most of these fall into three groups, the stylet, echinostome and forked-tailed cercariæ. The former group bear evidence of relationship to the Plagiorchiidæ; the echinostome cercariæ are known to be larval Echinostomidæ, and the forked-tailed cercariæ are probably larval schistosomes. The life history of only one species in the group has been worked out with certainty, that of *Cercaria Lissorchis fairporti*, with *Planorbis trivolvis* as larval host, a chironomid larva as intermediate host, and *Ictiobus* spp. as definitive hosts. Of the species recorded

TABLE II

RECORD OF MOLLUSK INFECTION WITH CERCARIÆ

Host Species	Total No. Species	Mono-stome	Amphis-tome	Distome	Holo-stome	Distinct Localities
Planorbis trivolvis	14	0	3	11	0	7
Planorbis parvus	3	1	0	2	0	1
Campeloma decisum	3	0	0	3	0	1
Lymnæa sp.	1	0	0	1	0	1
Lymnæa proxima	8	2	0	6	0	1
Lymnæa emarginata angulata	1	0	0	1	0	1
Lymnæa elodes	1	0	0	1	0	1
Lymnæa stagnalis	1	0	0	0	1	1
Lymnæa stagnalis appressa	1	0	0	1	0	1
Lymnæa stagnalis perambla	1	0	0	1	0	1
Lymnæa reflexa	3	0	0	3	0	1
Physa gyrina	19	3	0	15	1	5
Physa anatina	1	0	0	1	0	1
Physa heterostropha	1	1	0	0	0	1
Physa integra	1	0	0	1	0	1
Physa ancillaria	1	0	0	1	0	1
Goniobasis pulchella	1	1	0	0	0	1
Goniobasis virginica	2	0	0	2	0	1
Pleurocerca elevatum	1	0	0	1	0	1
Galba catascopium	1	0	0	0	1	1
Helix alternata	1	0	0	1	0	1
Helix albolabris	1	0	0	1	0	1
Anodonta cataracta	1	0	0	1	0	1
Anodonta marginata	1	0	0	1	0	1
Free-swimming only	3	0	1	2	0	3
Total No. distinct host records	72	8	4	57	3	
In two or more hosts	11	2	0	9	0	
Net species	61	6	4	48	3	

for the United States only one, *C.* (*Tetracotyle*) *typica* Diesing, 1858, is recorded for another locality than North America.

The larval hosts are without exception mollusks. All except two, *Anodonta cataracta* and *A. marginata,* are Gasteropoda. Several of the species have been found in two snails, although none have been recorded as infecting three or more hosts. Usually where the species occurs in two hosts the infection of the one is more widely spread and heavier than that of the other. Several records show the parasitism of several species of cercariæ within the same host species in the same locality. In fact, the writer found as many as four trematode species within the same host individual (*Planorbis trivolvis*) at DeKalb, Illinois, in August, 1917. The occurrence of two cercariæ species in the same host individual is commonly found in the records. In this case one of the parasites usually has a heavier hold on the host than the other and constitutes the major infection.

Limited geographical areas have been covered in the surveys for cercariæ. Two drainage systems of the Atlantic slope, isolated regions around the Great Lakes, a portion of the upper Columbia and an isolated region in Wyoming, together with more widely investigated areas in the Mississippi basin, constitute the localities in which collections have been made. The entire south, southeast and southwest constitute vast unexplored areas, the former two of which should yield a great number of species. In addition, the variation of species of flukes in snails from one season to another makes it highly probable that many more species occur in the Mollusca of the areas surveyed than the records show. Table I shows that one distome species, *Cercaria megalura*, has been found in *Goniobasis virginica* from the Atlantic slope, and in *Pleurocerca elevatum* from the Mississippi basin; and that *C. inhabilis* and *C. diastropha* have been found on both the eastern and western slopes of the Mississippi drainage. On the other hand, none of the species described for the Bitter Root Valley have been recorded east of the Rocky Mountains.

Records of percentage of infection from larval flukes vary from a few hundredths of a per cent. for certain cercariæ described by Sisnitzin in 1911 from the Black Sea to a heavy infection of every individual of a particular species in a locality. The lowest infection record for the United States is one per cent. (*C. fusiformis* in *Physa gyrina*). On the other hand, several heavy infections have been recorded, including three with total infection. The mollusks most heavily infected are the ubiquitous species, *Planorbis trivolvis* and *Physa gyrina*, and the western species, *Lymnæa proxima*. In the case of the *Planorbis* and the *Lymnæa* the average heavy infection is caused by distome cercariæ. The heavy infection among the physas is caused by monostome and holostome larvæ.

Table II, which summarizes the infection from the host point of view, shows that *Lymnæa proxima* has the greatest number of species per habitat. *Planorbis trivolvis* has been found to be infected in the greatest number of localities, while *Physa gyrina* is the only mollusk to harbor three groups of *Digenea*. Of the sixty named species listed in Tables I and II eleven are recorded from two hosts.

Accompanying the cercariæ in the mollusks are the parthenitæ (sporocysts and rediæ) of these cercariæ. The cercariæ develop parthenogenetically within these parthenitæ. Typically, as in

the life history of *Fasciola hepatica,* the sporocyst and redia generations both occur, but in several groups, notably in the stylet cercariæ and the furcocercariæ the redia stage has been omitted or replaced by another sporocyst stage.

Sporocysts and rediæ have not been sufficiently distinguished. The sporocyst is an adult which has lost its digestive tube, while a redia is an adult which possesses both a rhabdocœle gut and a pharyngeal sphincter. In certain sporocysts the sphincter still remains, as in *C. dendritica.* In other sporocysts, as in some furcocercariæ, while no definitely differentiated sphincter is present, the anterior end of the sac is muscular, turning in and out like the finger of a glove. This may easily be mistaken for a rhabdocœle gut.

The cercariæ develop within the parthenitæ and usually at the time of maturity break out of the parent and work their way through the tissues of the host into the water. In case no suitable host is at hand in which the larvæ may continue development they ordinarily encyst. Groups like the furcocercariæ, however, are not known to encyst. On the other hand, the writer has found encysted larvæ of *C. biflexa* within the larval host and encysted larvæ of *C. micropharynx* even within the parent sporocysts.

The parthenitæ of monostome, amphistome and holostome cercariæ are rediæ. Parthenitæ of certain groups of distome cercariæ are sporocysts and of other groups of distome cercariæ are rediæ, although some of the records are conflicting. This shows the need of the accurate determination of the parthenita of each cercaria, since the parthenita is a distinct generation in the life history of the species.

In order that the records may not be confusing the writer proposes the name *Cercaria gracilescens* for *C. gracilis* O'Roke 1917, preoccupied by La Valette 1855, and *C. minima* for *C. minor* Faust 1918, preoccupied by Lebour 1912.

In conclusion, the effect of the larva on the mollusk must be emphasized. It is an observable fact that heavily infected snails die sooner than uninfected ones. The cause of this mortality is both the mechanical disruption of the tissues of the infected mollusk and the pathological changes within the cells of the infected animal. A pathologico-chemical study of this relationship would be of great value to parasitologist and malacologist alike.

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